

INTERSEXUAL NICHE PARTITIONING IN DOWNY WOODPECKERS

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Rand (1952) proposed that sexual dimorphism facilitated attraction between males and females, inhibited mismating, and in some situations permitted differential niche use reducing dietary overlap and thus competition. Selander (1966) demonstrated a relationship between the degree of sexual dimorphism and sexual divergence in foraging behavior in 2 melanerpine woodpeckers, the insular Hispaniolan Woodpecker (*Melanerpes striatus*) and the continental Golden-fronted Woodpecker (*M. aurifrons*). He hypothesized that in continental avian communities the extent of sexual divergence in niche use would be limited owing to the relative richness of the avifaunas (see also Wallace 1974).

Since Selander's (1966) seminal paper, several investigators have quantified foraging differences in continental areas between sexes, especially in the Picidae (Jackson 1970, Kilham 1970, Willson 1970, Kisiel 1972, Grubb 1975, Williams 1975, Jenkins 1979). Foraging differences are not always associated with morphological divergence (Ligon 1968, Jackson 1970, Kisiel 1972). In this study, I examine the relationship between sexual dimorphism and intersexual niche partitioning of Downy Woodpeckers (*Dendrocopos pubescens*) living in different habitats and in different competitive environments. Further, I report a controlled experiment testing the premise that foraging differences between sexes are reduced by increased interspecific competition.

STUDY AREAS AND METHODS

Hart Memorial Woods, situated along the Sangamon River near Mahomet, Champaign Co., Illinois contained 2 distinct types of woodland—a relatively dry upland area (9.6 ha), and a wetter floodplain (3.4 ha). My third study site, an upland forest called Monen Woods (5.9 ha), was separated from Hart upland by a lowland strip 100 m wide. Analysis of vegetation composition and vertical structure for each area is presented in Williams (1977). Hart and Monen uplands are dominated by black (*Quercus velutina*), red (*Q. rubra*) and white (*Q. alba*) oaks; the lowland by silver maple (*Acer saccharinum*). Relative availability based on basal area of each tree species is presented in Table 2. With a density of 553.7 and 565.3 trees/ha, respectively, Hart and Monen uplands were similar. The floodplain, with 239.9 trees/ha, had an open canopy owing to loss of many large elms (*Ulmus* sp.) 15 years earlier (Root et al. 1971).

Habitat use was measured by 4 variables: (1) tree species occupied; (2) height of bird in tree; (3) condition of substrate (dead or alive); and (4) limb diameter. Observations were recorded on activity of the bird and habitat use at 10 sec signals given by an electronic metronome as suggested by Wiens et al. (1970). I collected data an average of 10 days each

month. After a bird was located, I allowed several min for habituation to my presence, timed the bird for no longer than 5 min and then found a new bird. This method reduced the sample size somewhat, but it also reduced bias by including observations from as many different individuals as possible.

Activities were categorized as follows (modified from Ficken and Ficken 1966, Jackson 1970, Willson 1970): (1) perch—no observable behavior taking place; (2) scale—pedal movement (horizontal or vertical), usually in search of food; (3) peck—repeated pecking in same location in tree; (4) bark probe—poking bill into cracks and crevices of bark; (5) fly—bird in flight; (6) ground forage—walking or hopping on ground, usually in search of food; (7) unknown—behavior unobservable at the signal; and (8) other—any other activity, such as display, preen, etc.

Foraging activity graphs were constructed using relative amounts of time spent on different foraging tactics. Perching is included in these graphs because birds stop during a foraging bout and study the bark surface.

Visual estimates of height were made for each bird; occasionally height estimates were checked with a forester's altimeter. For determinations of limb diameters I used the size of the bird being observed as a reference.

Niche breadths (B_j), or tendencies to specialize along a particular resource dimension, were calculated using the formula of Levins (1968). To simplify comparison of niche breadth values where different numbers of categories were involved, I scaled the values (Fager 1972) so that $B_{\max} = 1$ and $B_{\min} = 0$.

Overlap values on each niche dimension were calculated using Schoener's index (1968). Total overlap along a dimension yields a value of 1, complete separation yields a value of 0.

In addition to a monthly census of each area, I kept detailed notes on movements by individual Downy Woodpeckers. Thus, I estimated that 4 different individuals occupied Hart upland and lowland during both winters. In Monen upland, at least 4 different birds were observed during the winters of 1974–1975 and 1975–1976.

Morphological measurements were taken following Baldwin et al. (1931). Tongues were measured fully extended from the tip to the distal edge of the glottis (Lucas 1895). Methods for assessment of foods eaten by male and female Downy Woodpeckers are given in Williams and Batzli (1979a).

Elsewhere (Williams and Batzli 1979b), I have shown that the aggressive actions of Red-headed Woodpeckers (*M. erythrocephalus*) cause Downy Woodpeckers to forage lower in the canopy in upland habitats. During the winter of 1973–1974, oak trees produced few acorns and Red-headed Woodpeckers vacated my study areas, but during the winter of 1974–1975 with a relatively large acorn crop, Red-headed Woodpeckers dominated both Hart and Monen upland (for similar circumstances see Graber and Graber 1979). Only 2 Red-headed Woodpeckers established territories in Hart lowland during the winter of 1974–1975. This natural experiment allowed me to examine intersexual niche partitioning in an upland forest under 2 different competitive environments. Further, in early January 1975, I removed all Red-headed Woodpeckers from Monen upland and subsequently monitored the foraging of male and female Downy Woodpeckers in both Monen and Hart uplands. Red-headed Woodpeckers remained in Hart upland which served as a control area.

RESULTS

To determine the degree of sexual dimorphism, I compared mean values for 7 characters from 18 males and 12 females taken in central Illinois in 1975. Unlike Willson (1970), I did not find a significant difference in bill

TABLE 1

INTERSEXUAL COMPARISON OF MENSURAL CHARACTERS (MM) FOR MALE AND FEMALE
DOWNY WOODPECKERS IN CENTRAL ILLINOIS

	DW-M	DW-F		DW-M	DW-F
N	18	12	Tongue length	38.8 ± 0.78	35.0 ± 0.51*
Weight (g)	27.8 ± 0.45 ^a	27.0 ± 0.42	Wing length	125.2 ± 1.1	126.6 ± 1.6
Bill length	14.0 ± 0.16	13.8 ± 0.22	Span of foot	26.8 ± 0.22	26.4 ± 0.23
Bill width	5.2 ± 0.15	5.0 ± 0.20	Tarsal length	14.4 ± 0.23	13.9 ± 0.34

^a $\bar{x} \pm SE$.

* Difference between sexes significant at $P < 0.05$ level.

length between sexes. Interestingly, tongue length for males and females was significantly different (Table 1).

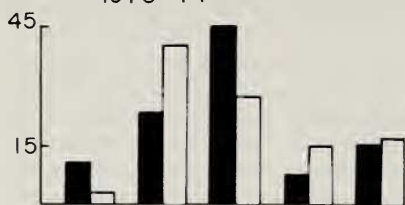
Foraging activity patterns of males and females diverged in Hart upland and lowland for both winters (Fig. 1, $P < 0.01$ in all cases). Males pecked for prey items more than females, whereas females probed bark crevices more. When Red-headed Woodpeckers were experimentally removed from Monen upland, divergence patterns between the sexes were similar in the experimental and control areas. Males pecked for food more, but females bark-probed more often.

Males and females selected different tree species on both study areas of Hart Woods during both winters (Table 2, $P < 0.01$ in all cases). When Red-headed Woodpeckers emigrated from Hart upland, males preferred black and red oaks, whereas females selected the morphologically distinct white oak most of the time. The shift of both males and females to understory trees in this area in 1974–1975 was in part because Red-headed Woodpeckers controlled the upper canopy and compelled both sexes to forage lower (Williams and Batzli 1979b). In Hart lowland, females favored maple more than did males for both years, but males chose fallen logs and standing dead trees most often during the winter of 1973–1974. The following winter, when only 2 Red-headed Woodpeckers established territories in the lowland, males foraged more often on maples and honey locust (*Gleditsia triacanthos*) trees. Comparing data from the experimental and control areas, both sexes used white oaks in the control area less, which was probably a result of decreased availability of that species (Table 2). In addition, both sexes used understory trees more in the control area because they were compelled to forage lower in the canopy.

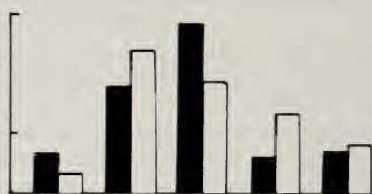
Sexual divergence along the foraging height dimension was disparate between years and habitats (Fig. 2, $P < 0.01$ in all cases). During 1973–1974, when Red-headed Woodpeckers were absent from the upland, male

HART UPLAND

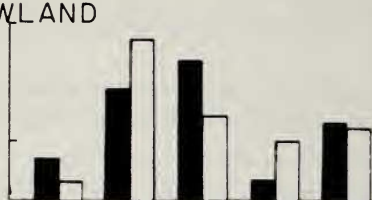
1973 - 74



1974 - 75



HART LOWLAND



REMOVAL EXPERIMENT

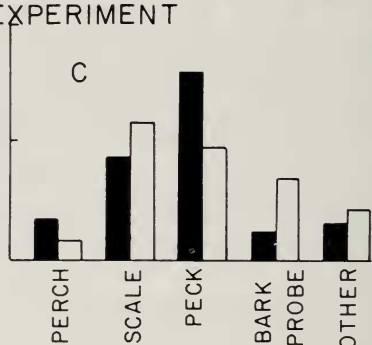
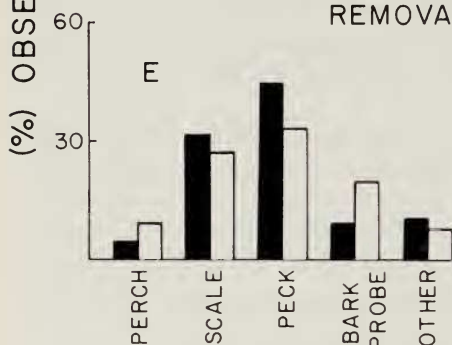


FIG. 1. Foraging activity graphs for male (solid bars) and female (open bars) Downy Woodpeckers from 2 habitats and during an experiment in which Red-headed Woodpeckers were removed from the experimental area (E), but allowed to remain in the control area (C). Sample sizes are the same as in Table 2.

and female Downy Woodpeckers foraged in the upper canopy most of the time, but when Red-headed Woodpeckers were present the following year, males and females more often exploited the lower portions of the canopy. In addition, males and females seemed to diverge more along the height dimension in the presence of Red-headed Woodpeckers. Because of the low numbers of Red-headed Woodpeckers in the lowland during 1974-1975, the impact of their dominance on foraging patterns of Downy Woodpeckers was slight. Males tended to ground forage more in this area during

TABLE 2

TREE SPECIES USED BY BOTH SEXES OF DOWNY WOODPECKERS DURING 2 WINTERS AND DURING AN EXPERIMENT IN WHICH RED-HEADED WOODPECKERS WERE REMOVED

Tree species	Avail- ability ^a	1973-1974		1974-1975	
		DW-M	DW-F	DW-M	DW-F
Hart upland					
		(730) ^b	(652)	(172)	(791)
Black and red oak	0.55	0.36	0.08	0.40	0.12
White oak	0.33	0.46	0.88	0.24	0.66
Bitternut hickory (<i>Carya cordiformis</i>)	0.02	0.04	—	0.13	†
Understory trees	0.03	0.06	0.02	0.19	0.09
Fallen logs	0.06	—	—	—	0.03
Shagbark hickory (<i>C. ovata</i>)	†	0.03	†	0.02	0.08
Standing dead	†	0.02	—	†	†
Other	†	0.02	0.02	0.01	†
Hart lowland					
		(339) ^b	(302)	(551)	(629)
Silver maple	0.26	0.14	0.36	0.30	0.33
Logs	0.24	0.38	0.33	0.03	0.09
Bur oak (<i>Quercus macrocarpa</i>)	0.13	—	—	0.02	0.32
Green ash (<i>Fraxinus pennsylvanica</i>)	0.11	0.07	0.04	0.12	0.08
Standing dead	0.07	0.16	0.06	0.06	0.03
Hackberry (<i>Celtis occidentalis</i>)	0.06	0.09	0.03	0.06	0.01
Black walnut (<i>Juglans nigra</i>)	0.03	—	0.02	†	0.01
American and red elm	0.03	0.05	†	0.10	0.07
Bitternut hickory	0.02	†	—	0.03	—
Hawthorns (<i>Crataegus</i> sp.)	0.02	—	—	—	—
Sycamore (<i>Plantanus occidentalis</i>)	0.01	—	0.04	—	0.02
Honey locust	0.01	0.02	0.04	0.23	—
Other oaks	†	0.08	0.02	†	0.02
Other	†	†	0.05	0.04	0.02
Removal experiment					
Experiment	Control	Experiment		Control	
		(370) ^b	(725)	(378)	(647)
Black, red oak	0.47	0.55	0.11	0.69	0.10
White oak	0.39	0.33	0.84	0.14	0.66
Understory trees	0.02	0.03	—	0.10	0.10
Fallen logs	0.07	0.06	—	—	0.04
Shagbark hickory	†	†	—	0.01	0.09
Standing dead	0.05	†	—	0.02	†
Other	†	0.01	—	0.04	0.01

^a Availability index based on basal area/ha.

^b Number of observations.

† Trace.

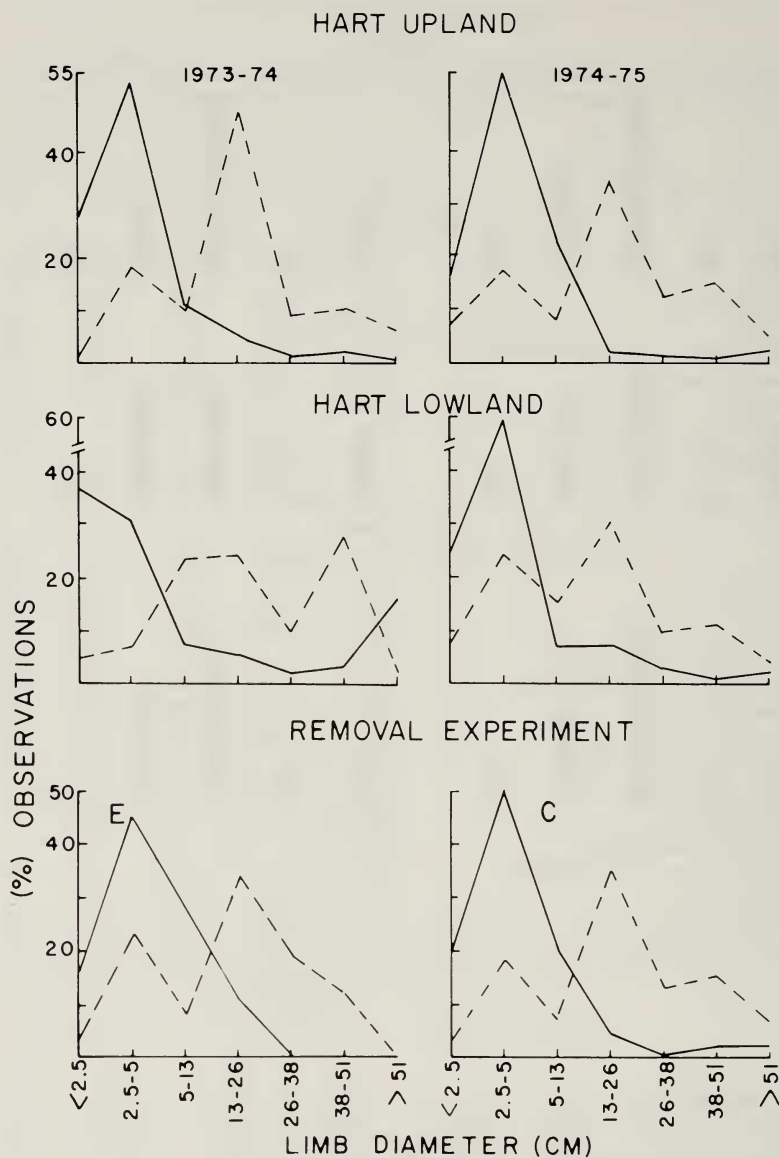


FIG. 2. The use of heights by male (solid lines) and female (dashed lines) Downy Woodpeckers in 2 habitats and during an experiment in which Red-headed Woodpeckers were removed from the experimental area (E), but allowed to remain in the control area (C). Sample sizes are the same as in Table 2.

both winters. In the experimental area both sexes shifted to higher portions of the canopy, but in the control area males diverged from females by foraging both high and low in the canopy.

Selection of living versus dead substrate by males varied, but was always different from females ($P < 0.05$ in all cases). Females foraged over living substrate more often in both areas for both years. I found no apparent shift in substrate use by the sexes between experimental and control areas.

For limb diameter use, males consistently hunted for prey on smaller limbs than did females (Fig. 3). Males selected smaller limbs than females regardless of their foraging height distribution. Even though males and females altered their foraging height patterns in the experimental area, no observable shift was noted in limb diameter use. In harmony with previous data, males perused small limbs for prey more often than did females in both the experimental and control area.

Niche breadth values showed males and females using tree species more evenly when Red-headed Woodpeckers were present in the upland (Table 3). Males tended to be more generalized than females on tree species in all areas in the presence or absence of Red-headed Woodpeckers. Males were more specialized for limb diameters in all situations. A noticeable shift in niche breadth patterns in the experimental area occurred for both sexes along the height dimension. Males and females were more generalized in the presence of a competitor. Also, males and females exploited live and dead substrate more evenly in the experimental area, although relative substrate availability was not measured in either area. Females were more specialized in tree species use in the experimental area.

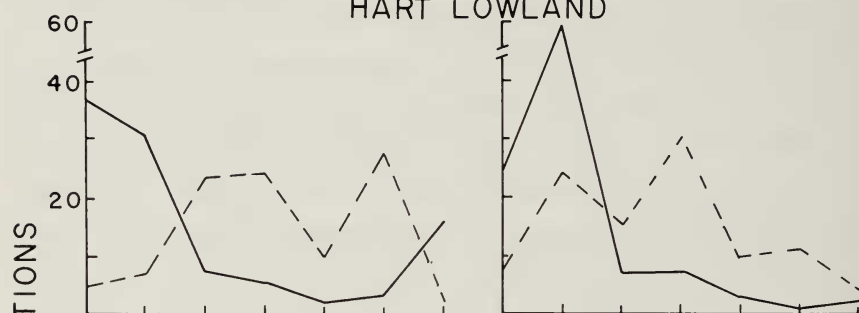
Overlap values revealed that sexes separated more along the tree species and height dimensions when Red-headed Woodpeckers occupied the upland (Table 4). Comparing experimental and control areas, sexes showed less overlap along the foraging activity, tree species, height and limb diameter dimensions in the control area where dominant Red-headed Woodpeckers were present.

Because of a mast crop failure in the fall of 1975, Red-headed Woodpeckers emigrated from my experimental area (Monen upland). To examine how male and female Downy Woodpeckers would forage when Red-headed Woodpeckers were naturally removed from this area, I observed their feeding behavior during January and February of 1976 (56 observations for males, 423 for females). I noted consistent patterns compared to the previous winter when Red-headed Woodpeckers were experimentally removed. Males excavated more than females, but females bark-probed more. Females concentrated on white oaks but males preferred black, red

HART UPLAND



HART LOWLAND



REMOVAL EXPERIMENT

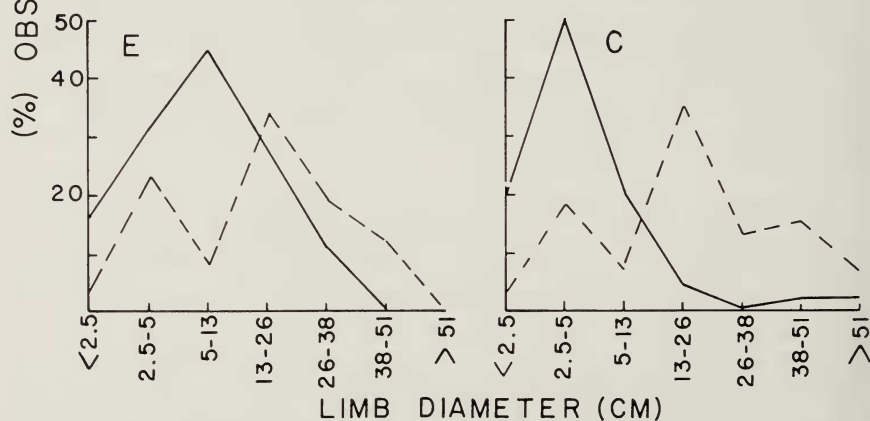


FIG. 3. The use of limb diameters by male (solid lines) and female (dashed lines) Downy Woodpeckers in 2 habitats and during an experiment in which Red-headed Woodpeckers were removed from the experimental area (E), but allowed to remain in the control area (C). Sample sizes are the same as in Table 2.

TABLE 3

NICHE BREADTH VALUES FOR MALE AND FEMALE DOWNY WOODPECKERS DURING 2 WINTERS AND DURING AN EXPERIMENT IN WHICH RED-HEADED WOODPECKERS WERE REMOVED

Category	Hart upland				Hart lowland				Removal experiment			
	1973-1974		1974-1975		1973-1974		1974-1975		Experiment		Control	
	M	F	M	F	M	F	M	F	M	F	M	F
Activity	0.34	0.35	0.36	0.44	0.57	0.45	0.42	0.40	0.55	0.79	0.56	0.77
Tree species	0.19	0.03	0.29	0.12	0.29	0.23	0.35	0.25	0.16	0.07	0.16	0.20
Height	0.76	0.48	0.67	0.79	0.22	0.55	0.79	0.79	0.16	0.58	0.67	0.67
Dead or alive	0.99	0.63	0.98	0.63	0.72	0.99	0.55	0.65	0.64	0.24	0.96	0.82
Limb diameter	0.28	0.40	0.27	0.68	0.49	0.64	0.25	0.67	0.36	0.57	0.29	0.64
Mean	0.51	0.38	0.51	0.53	0.46	0.59	0.47	0.55	0.37	0.45	0.53	0.62

and white oaks. Patterns for height and limb diameter use duplicated those from the experimental site for the previous winter.

The diet of Downy Woodpeckers in central Illinois during winter collectively consists of about 60% animal material (Williams and Batzli 1979a), but significant differences existed between males and females (χ^2 , $P < 0.005$). Males consumed more Hymenoptera (mostly Formicidae) (22% vs 12%), corn (*Zea mays*) (23% vs 15%), and poison ivy (*Rhus radicans*) seeds (9% vs 4%); females had more homopterans (5% vs 11%), spiders (Araneida) (1% vs 10%), and wheat (*Triticum aestivum*) (1% vs 5%) in their diets. Intersexual overlap values for the food, calculated to be

TABLE 4

NICHE OVERLAP VALUES ALONG 5 DIMENSIONS FOR MALE AND FEMALE DOWNY WOODPECKERS DURING 2 WINTERS AND DURING AN EXPERIMENT IN WHICH RED-HEADED WOODPECKERS WERE REMOVED

Category	Hart upland		Hart lowland		Removal experiment	
	1973-1974	1974-1975	1973-1974	1974-1975	Experiment	Control
Activity	0.70	0.78	0.76	0.73	0.82	0.76
Tree species	0.57	0.49	0.65	0.57	0.56	0.36
Height	0.63	0.58	0.59	0.78	0.60	0.53
Alive or dead	0.73	0.71	0.79	0.96	0.56	0.76
Limb diameter	0.36	0.38	0.32	0.49	0.46	0.36
Mean	0.60	0.59	0.62	0.71	0.60	0.55

0.61, were not appreciably greater than interspecific comparisons for the bark-foraging guild during winter (Williams and Batzli 1979a).

DISCUSSION

The hypothesis that the sexes of Downy Woodpecker partition the overall niche of the species into subniches is supported by the data in this report. The pattern which emerges, that males forage more by pecking, use a wider array of tree species and search smaller limbs, appears to be consistent regardless of habitat or competitive environment. Where Downy Woodpeckers forage along the vertical dimension depends not only on habitat type but also the competitive environment. Grubb (1975) has suggested that weather factors may also influence the vertical foraging patterns of Downy Woodpeckers.

Other investigators have witnessed similar patterns. Kisiel (1972), collecting data for Downy Woodpeckers in maple-beech-hemlock forests of eastern New York, wrote that males excavated more than females and that they were more frequently observed on smaller limbs. Recording observations in Brownfield woods during winter in central Illinois, Willson (1970) wrote that males chose small limbs significantly more than did females. She did not observe differences in foraging technique. From data taken in Kansas, Jackson (1970) also observed males more often on smaller limbs. In an earlier paper, I noted foraging patterns during early spring consistent with those discussed in this presentation (Williams 1975).

Kilham (1970) speculated that male Downy Woodpeckers foraging higher in the canopy signified dominance over females. My data do not support this hypothesis, but rather suggest that vertical foraging patterns in both sexes are influenced by a complex set of variables such as habitat structure, food availability at various heights and the competitive environment. However, males do consistently peck on smaller limbs for food items than do females. Perhaps selection has acted to separate males from females by choosing male genotypes which are more efficient at extracting (by pecking) prey items from smaller limbs. Their longer tongues may indicate that males take prey from deeper within the foraging substrate. Conversely, females may be more efficient at probing for insects within bark crevices.

Tree species selection may simply be a reflection of foraging efficiencies of the respective genotypes. If female genotypes are more efficient at bark-probing, then one would expect them to choose more rough-barked tree species (i.e., white oaks), which almost certainly harbor more insects than do smooth-barked species.

Dietary analysis for the sexes of Downy Woodpecker during winter does

indicate that differential foraging techniques allow acquisition of different food resources, thus reducing competition. I have shown elsewhere that Brown Creepers (*Certhia familiaris*) eat mostly small homopterans during winter and that they forage by probing crevices in bark on trunks and larger branches (Williams 1977). I suggest here that in upland forests female Downy Woodpeckers consume more homopterans and spiders because they probe more in bark crevices. Conversely, males take more ants by pecking into small limbs and removing them with a longer tongue.

Selander (1966) posited that greater intersexual structural dimorphism and behavioral divergence occurs for insular woodpeckers compared to mainland forms because of a reduced competitive environment on islands. With fewer competitors, insular populations increased and subsequently expanded their niches. When food became limiting, selection favored establishment of subniches for the sexes. These ideas are based on long-term evolutionary responses of populations under different competitive regimes. My data point out short-term niche shifts by both sexes of the Downy Woodpecker under different competitive environments. In upland forests with increased interspecific competition, both sexes decreased overlap along several niche dimensions. If food is most likely to be in short supply during this period (see Williams 1977), then when Downy Woodpeckers are restricted to the lower canopy by interference from Red-headed Woodpeckers, perhaps sexes diverge to reduce competition for food. When the competitor was removed (Red-headed Woodpeckers) both males and females shifted to higher zones in the canopy. Since more limbs and branches occur in the upper zones (Williams 1977), food may have been more abundant there, allowing greater overlap in space between sexes.

SUMMARY

I studied intersexual niche partitioning of a relatively monomorphic population of Downy Woodpeckers in central Illinois during 3 winters and in 2 different habitats. By comparing the foraging patterns of male and female Downy Woodpeckers during the winters of 1973–1974 and 1975–1976 when Red-headed Woodpeckers were absent, to their foraging patterns during the winter of 1974–1975 when Red-headed Woodpeckers were present, I examined the influence of competition on intersexual niche partitioning in upland habitats. Additionally, I observed the foraging of males and females in an upland area where Red-headed Woodpeckers were experimentally removed and compared those differences to patterns in a control area where Red-headed Woodpeckers remained. Results showed that male Downy Woodpeckers usually pecked for food on small limbs, but females more often probed bark crevices of trunks and larger branches regardless of habitat or competitive environment. In upland forests, males chose black, red and white oaks, but females preferred white oak. In the lowland females more often selected maples, whereas males more often foraged on fallen logs and standing dead trees during the winter of 1973–1974. Males shifted to maples and honey locust trees during the winter of 1974–1975. When Red-headed Woodpeckers occupied

the upland forest, both sexes foraged lower in the canopy and more often used understory trees. Sexes diverged more along the height dimension in the presence of Red-headed Woodpeckers, seemingly reducing interspecific competition. Analysis of diets revealed that males consumed more ants, whereas females ate more homopterans.

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Errata.—Vol. 92, No. 1, "Bi-parental care in Killdeer: an adaptive hypothesis" by Sarah Lenington. On p. 18 the scientific name for Great Knot should read *Calidris tenuirostris* and the scientific name for Green Sandpiper should read *Tringa ochropus*.

"The selection and use of fruit by birds in an eastern forest" by John W. Baird. On p. 69 the scientific name for Red-bellied Woodpecker should read *Melanerpes carolinus*.

"Spatial and temporal distribution of rails in Colorado" by Herman J. Giese, Ronald A. Ryder and Clait E. Braun. On p. 96 the scientific name for Yellow Rail should read *Coturnicops novaboracensis*.

"Food habits of White Pelicans during 1976 and 1977 at Chase Lake National Wildlife Refuge" by Gary R. Lingle and Norman F. Sloan. On p. 124 the scientific name for fathead minnow should read *Pimephales promelas*.

Vol. 92, No. 2, "Nest predation by the speckled king snake" by Charles F. Facemire and Stephen D. Fretwell. On p. 250 the scientific name for Red-winged Blackbird should read *Agelaius phoeniceus*.

Credit for the photograph for the Frontispiece of the Magellanic Oystercatcher (*Haematopus leucopodus*) should go to Dr. Joseph Jehl, Jr.

Vol. 92, No. 3, "Nest placement in Sage Thrashers, Sage Sparrows and Brewer's Sparrows" by Terrell Rich. On p. 263, Table 1, the first value under Sage height (cm) should read 67.1 ± 8.4^b .

"A Paint-billed Crake in Virginia" by Charles R. Blem. On p. 393 the scientific name of the Spotted Rail should read *Paradiralus maculatus*.

"The influence of agriculture on avian communities near Villavicencio, Colombia" by Wallace D. McKay. On p. 384 the common name of *Forpus conspicillatus* should read Spectacled Parrotlet.

"Back carrying of young by Trumpeter Swans" by Theodore Bailey, Edward Bangs and Vernon Berns. On p. 413 the scientific name of Black-necked Swan should read *Cygnus melanocoryphus*.